Multilevel Organisation of Animal Sociality

Grueter, Cyril C ; Qi, Xiaoguang ; Zinner, Dietmar ; Bergman, Thore ; Li, Ming ; Xiang, Zuofu ; Zhu, Pingfen ; Migliano, Andrea Bamberg ; Miller, Alex ; Krützen, Michael ; Fischer, Julia ; Rubenstein, Daniel I ; Vidya, T N C ; Li, Baoguo ; Cantor, Maurício ; Swedell, Larissa

DOI: https://doi.org/10.1016/j.tree.2020.05.003

Multilevel organisation of animal sociality

Cyril C. Grueter*, Xiaoguang Qi, Dietmar Zinner, Thore Bergman, Ming Li, Zuofu Xiang, Pingfen Zhu, Andrea Bamberg Migliano, Alex Miller, Michael Krützen, Julia Fischer, Daniel I. Rubenstein, T. N. C. Vidya, Baoguo Li, Maurício Cantor and Larissa Swedell

CCG: School of Human Sciences, The University of Western Australia, Perth, WA 6009, Australia
CCG: Centre for Evolutionary Biology, School of Biological Sciences, The University of Western Australia, Perth, WA 6009, Australia
XQ: Shaanxi Key Laboratory for Animal Conservation, College of Life Sciences, Xi'an, 710069, Chi
DZ: Cognitive Ethology Laboratory, German Primate Center (DPZ), Leibniz Institute for Primate Research, 37077 Göttingen, Germany
DZ: Leibniz ScienceCampus for Primate Cognition, Göttingen, Germany
TB: Department of Psychology, University of Michigan, Ann Arbor, USA
TB: Department of Ecology and Evolutionary Biology, University of Michigan, Ann Arbor, USA
ML: CAS Key Laboratory of Animal Ecology and Conservation Biology, Institute of Zoology, Chaoyang District, Beijing 100101, China
ML: Center for Excellence in Animal Evolution and Genetics, Chinese Academy of Sciences, Kunming, China 650223
ZX: College of Life Science and Technology, Central South University of Forestry and Technology, Changsha, Hunan 410004, China
PZ: CAS Key Laboratory of Animal Ecology and Conservation Biology, Institute of Zoology, Chaoyang District, Beijing 100101, China
ABM: Department of Anthropology, University of Zurich, 8057, Zürich, Switzerland
AM: School of Human Sciences, The University of Western Australia, Perth, WA 6009, Australia
MK: Department of Anthropology, University of Zurich, 8057, Zürich, Switzerland
JF: Cognitive Ethology Laboratory, German Primate Center (DPZ), Leibniz Institute for Primate Research, Kellnerweg 4, 37077 Göttingen, Germany
JF: Department for Primate Cognition, Georg-August-University of Göttingen, Göttingen, Germany
DR: Department of Ecology and Evolutionary Biology, Princeton University, Princeton, NJ, USA
TNCV: Evolutionary and Organismal Biology Unit, Jawaharlal Nehru Centre for Advanced Scientific Research (JNCASR), Jakkur, Bengaluru 560064, India
BL: Shaanxi Key Laboratory for Animal Conservation, College of Life Sciences, Xi'an, 710069, China
BL: Center for Excellence in Animal Evolution and Genetics, Chinese Academy of Science, Kunming, 650223, China
MC: Department for the Ecology of Animal Societies, Max Planck Institute of Animal Behavior, Konstanz, 78464, Germany
MC: Centre for the Advanced Study of Collective Behaviour, University of Konstanz, Konstanz, 78464, Germany
MC: Department of Biology, University of Konstanz, Konstanz, 78464 Germany
MC: Departamento de Ecologia e Zoologia, Universidade Federal de Santa Catarina, Florianópolis, 88048-970, Brazil
MC: Centro de Estudos do Mar, Universidade Federal do Paraná, Pontal do Paraná, 83255-000, Brazil
MC: School of Animal, Plant and Environmental Sciences, University of the Witwatersrand, Johannesburg, 2000, South Africa
LS: Department of Anthropology, Queens College, City University of New York, Flushing, NY 11367-1597, USA

LS: New York Consortium in Evolutionary Primatology, New York, NY, USA
LS: Anthropology, Biology and Psychology Programs, CUNY Graduate Center, 365 Fifth Avenue, New York, NY 10016, USA
LS: Department of Archaeology, University of Cape Town, Rondebosch 7701, Cape Town, South Africa

Abstract

Multilevel societies (MLSs)—stable nuclear social units within a larger collective encompassing multiple nested social levels—occur in several mammalian lineages. Their architectural complexity and size impose specific demands on their members requiring adaptive solutions in multiple domains. The functional significance of MLSs lies in their members being equipped to reap the benefits of multiple group sizes. Here we propose a unifying terminology and operational definition of MLS. To identify new avenues for integrative research, we synthesise current literature on the selective pressures underlying the evolution of MLSs and their implications for cognition, intersexual conflict, and sexual selection. Mapping the drivers and consequences of MLS provides a reference point for the social evolution of many taxa including our own species.

Keywords: multilevel society; social complexity; socioecology

Multilevel sociality in nature

Animal sociality reflects the interplay between attractive and repulsive forces—opportunities for reproduction, cooperation, protection and information acquisition are counterbalanced by competition and vulnerability to predators and pathogens [1]. One outcome of this interplay is a **social system** with multiple levels, a **multilevel society** (Glossary, hereafter MLS), comprising **core units** organized into increasingly inclusive entities. Understanding how these social constituents interact and coexist, and how dispersal shapes the resulting kinship structure across multiple levels, is fundamental to a holistic understanding of the evolution of these systems.

MLSs are best known from primates but have recently been reported in a range of animals [2-7]. Here we synthesise current knowledge on MLSs, critically evaluate their causes and consequences, and offer prospects for future research. We build from socioecological principles emphasizing ecological—resource distribution, predation threat—and social—kin selection, sexual conflict—factors in organising individuals and relationships in space and time [1]. We focus on Mammalia given the predominance of MLSs in this class. As this very system also characterises our own species, mapping the causes and consequences of MLSs provides a valuable reference point for tracing human social evolution.

Defining multilevel societies

MLSs are social systems characterised by nested social entities comprising a minimum of two discernible, consistent levels of social integration between the individual and the population (Fig. 1). The terms describing these nested social levels are inconsistent across species, thus, to facilitate comparison, we propose a standardized terminology: *core units* and *upper levels* for these two mandatory levels, and *intermediate levels* and *apex levels* for the facultative levels described below (Table 1).

In non-human primates, the primary entities of MLSs are usually small *core units* comprising one reproductive male and multiple females—called one-male units or OMUs [8]. In other mammals there is greater variability: in African elephants (*Loxodonta africana*) and sperm whales (*Physeter macrocephalus*), core units comprise closely associated breeding females

and their calves, with occasional male visitors [9, 10]. Core units are usually highly cohesive and stable: individuals show strong fidelity to their units, and socio-positive interactions are far more frequent within than between units [2, 11]. In terrestrial MLSs, core units are usually spatially discrete, defined by spatial and social proximity among members [12]. Closely associated core units may form a secondary, less consistent level of organization with various names [11, 13, 14], herein called an *intermediate level*.

For a system to be a MLS, in addition to core units there needs to be an *upper level* that is stable enough to be recognisable, despite variability in spatio-temporal cohesiveness [8]. Membership in an upper level can be consistent [15] or more probabilistic [13]. In primates, the upper level is often called 'band'. In some cases, upper levels coalesce to form even higher levels—herein called *apex levels*—that are distinctively larger and number several hundred to over thousand individuals. Apex levels can be induced by habitat features rather than social attraction; thus they do not always represent genuine social units.

The organisational complexity of MLSs is best exemplified by hamadryas baboons (*Papio hamadryas*), which exhibit four distinct social levels [14, 16, 17]. At the heart of their society are *core units,* called 'one-male units' (OMUs or 'harems'), consisting of a 'leader' male, multiple breeding females, and occasional follower males. Their *intermediate level* is the clan, consisting of two or more closely associated OMUs and solitary (unaffiliated) males. Clans are nested within bands (*upper levels*), the most visibly apparent, spatially cohesive level. Finally, troops (*apex level*) represent temporary associations of bands at sleeping cliffs. Other primate MLSs show a superficially similar **social organisation**, but the number and cohesion of nested levels varies.

To identify the boundaries of each social level, researchers rely on long-term empirical data and clustering or community detection methods (Box 1). While there are boundaries between core units, these are not impermeable and some individuals are socially connected across units. Occasionally, members of different units interact socially [18, 19], engage in joint patrolling [20], mingle [21], or copulate [22].

Shared space use can set the stage for the emergence of MLSs [3, 23, 24]. However, **aggregations** of social units without active social preferences—e.g. attracted to the same localised resource or co-occurring due to constraints of habitat structure—cannot be

considered MLSs, nor can social units that occasionally encounter and mingle non-agonistically [25] be MLSs, because these encounters are infrequent and transient.

The term 'multilevel society' is sometimes used interchangeably with '**fission-fusion,**' but this is a conceptual error. Fission-fusion is not a type of social system, but instead describes how social units cleave and coalesce over time to form subunits with variable size and composition [26]. Fission-fusion dynamics unfold over various time scales, from hours to months, and are generally found in MLSs [10, 12, 17] as well as in uni-level societies [27]. In non-MLSs, fission-fusion is individualistic and subunits vary widely in composition (*atomistic*), whereas in MLSs fission-fusion usually happen along the boundaries of the core units or intermediate levels without compromising the integrity of those units (*molecular*) [8, 28].

Taxonomic distribution

MLSs are relatively uncommon and patchily distributed on the mammal phylogenetic tree (Fig. 2). First described for hamadryas baboons in the pioneering study by Hans Kummer in the 1960s [17], they have subsequently been documented in other primates (papionins, colobines, humans), cetaceans, elephants, and equids [2, 10, 13, 29-31] (for a full list see Fig. 2). Some taxa show MLSs in only some ecological contexts (e.g. [2, 32]). Bottlenose dolphins (*Tursiops* sp.), for example, are generally characterized by atomistic fission-fusion dynamics [33]. Some populations, however, exhibit **multilevel alliances** among males embedded into an open fission-fusion network, with up to three levels of social integration between the individual and the population. In Shark Bay, males form stable 2nd-order alliances of 6-14 adult males. Nested within these 2nd-order alliances, two to three males form 1st-order alliances with varying composition for the purpose of coercing females in reproductive condition. To this end, Shark Bay dolphins deviate from our MLS definition in that the highly cohesive and stable units in Shark Bay dolphins occur on a higher level. Second-order alliance members may cooperate in attacking, or defending against, other 2nd-order alliances, sometimes even cooperating on a third level [34].

MLSs have been proposed for other mammal species, but some were based on vague definitions. For example, reticulated giraffe (*Giraffa camelopardalis*) are found in social

cliques embedded in larger subcommunities and communities and show partner preferences; however, the composition of core units (cliques) is highly variable [3]. Observations of members of different social units of western gorillas (*Gorilla gorilla gorilla*) interacting non-aggressively and co-visiting forest clearings have been used as evidence for MLSs [7, 35], but whether associations are durable across contexts remains poorly known.

Social dynamics within multilevel societies

The proximate mechanisms underlying MLSs can vary widely. Geladas and hamadryas baboons, for example, differ considerably in their micro-level **social structure**. In geladas, core units are shaped by kin bonds among closely related females [36] whereas in hamadryas baboons the pair bonds between a leader male and his females underpins core unit stability, with male-male bonds linking the higher social levels [17, 37]. Females are philopatric in geladas, whereas males are philopatric in hamadryas [11, 36, 38]. Guinea baboon MLSs are similar to those of hamadryas and geladas, but differ from hamadryas in the greater social freedom of females, and from geladas in the presence of male-male bonds across units [39].

MLSs can also shape the typically antagonistic social dynamics between breeding and bachelor males. In geladas, the presence and proximity of bachelors can exert a predator-like effect and cause spatial clumping of breeding units [40], whereas in snub-nosed monkeys proximity to breeding units reduces social cohesion among bachelor males [41], both reflections of male competition.

Evolution, maintenance and adaptive functionality

The evolutionary pathways leading to the emergence of MLS across mammalian taxa are variable. In hamadryas baboons, for example, phylogenetic reconstructions suggest that ancestral multimale-multifemale groups fractionated into OMUs with stable breeding bonds. Increased group sizes due to localised resources or greater predator pressure in open habitats may have elevated feeding competition, aggression, and harassment by unfamiliar individuals. To mitigate these costs, individuals would have formed subgroups,

with females tightening their relationships with a single male capable of protecting them [8, 42]. In colobine monkeys, by contrast, MLSs likely evolved via a merger of ancestrally autonomous OMUs [8], with persistent threat from potentially infanticidal bachelor males as a formative factor. Through communal defence or the safety-in-numbers effect, leader males could have collectively reduced bachelor threat, thereby prolonging their tenure and attenuating the risk of infanticide [23].

MLS maintenance requires a unifying social network spanning the boundaries of social units, and kinship has likely played a major role in shaping such networks. In hamadryas baboons, these links are provided by male-male social and kin relationships, evident at the clan level [14, 16, 38]. Similarly, strongly-bonded Guinea baboon males are more likely to be related, although kinship is not a prerequisite (Table 1) [43]. Another unifying force may be limitations on female dispersal to within the confines of the highest social levels, which may increase relatedness among females and strengthen tolerance among core units. This may explain occasional affiliative exchanges between females across units, as among snub-nosed monkeys [18] and hamadryas baboons [19]. Multi-year field studies suggest that kin selection among females can be an organising principle of MLSs. Female kinship predicts associations between gelada core units [36], and hamadryas females within core units are more closely related than expected despite being coercively transferred by males [44]. Similarly, aggregation of plains zebra family groups to reduce sexual harassment is driven by females, not males, and female half-siblings usually reside together [45]. Relatedness also predicts association between core units of African elephants [46], though it may be less instrumental in shaping social bonds within higher levels. In sperm whales, kinship influences social organisation within nearly-matrilineal social units, but associations between units are not strictly kin-based [47]. Future research on how kinship links core units in MLSs will elucidate both the maintenance and the evolutionary origins of these systems, with implications for the evolution of our own [42, 48].

In contrast to uni-level societies with one single optimal grouping size, in MLSs different functions can be optimised at different levels. Given that additional levels of sociality above the core unit can afford adaptive possibilities that core structures in isolation cannot, members of MLSs are well equipped to balance the costs and benefits of group-living [49]. . Hamadryas baboons illustrate how each social level makes possible different types of

collective interests shared among individuals: the core unit offers access to reproductive partners, the clan is a substrate for the maintenance of male-male relationships, the band serves an anti-predator and resource-defence function, and the troop optimises predator protection at sleeping sites while providing opportunities for gene flow via female takeovers [14, 17]. Reduction of predation through dilution or communal defence is likely a key driver of higher levels in many MLSs ([2, 50]; but see [23]). In zebras and some snub-nosed monkeys, males in OMUs that are part of a band, compared to those not in a band, are better able to prevent intrusions of coordinated bachelor males vying for reproductive opportunities [20, 29]. In African elephants, the highest 'level' may be an epiphenomenon or a by-product of individual predispositions to socially interact [10]; in contrast, for marine mammals—whose social lives depend on acoustic communication—the highest social level can provide the coarse-grained information needed to distinguish between familiar and unfamiliar conspecifics (Box 2). While atomistic fission-fusion dynamics provide an alternative means of flexibly responding to socioecological pressures [26], MLSs allow maintenance of core units, providing a greater consistency in social relationships and cleavage points.

Consequences of living in multilevel societies

MLSs bring new challenges and opportunities and may have follow-on effects in a variety of domains including male-male competition, intersexual conflict, and cognitive abilities. First, while male-male tolerance appears in many—but not all—MLSs, this does not preclude male-male competition. Mating competition in MLSs occurs in a context of close proximity among reproductive units and between reproductive units and bachelor males within the larger society. This crowded, competitive environment can also be fertile ground for the evolution of signals of male quality and physical prowess. For example, Asian colobine species with MLSs exhibit greater sexual dimorphism in body mass (a key indicator of male-male competition) than those without MLSs [51]. A comparative analysis among primates, controlled for phylogeny and group size, revealed that sexually dimorphic ornaments are also most pronounced in MLSs compared to other societies [52]. Such ostentatious traits include the mantles of hamadryas and Guinea baboons, red chest patches of geladas, extended noses of proboscis monkeys, and red lips of black-and-white snub-nosed monkeys

(Fig. 2f). These traits likely allow males to quickly, reliably and remotely assess the fighting ability of competitors, while females can gauge the quality of potential mates. Such ornaments are adaptive when individuals are confronted with a high density of competitors and surrounded by unfamiliar conspecifics [52, 53].

One form of sexual conflict generated by asymmetry in reproductive investment is infanticide, common when the highest ranking or sole male in a social unit is replaced, to which females may mount behavioural defences [54]. In MLSs, these counterstrategies include paternity concentration (long-lasting associations with a bodyguard) and paternity confusion (to prevent infanticide from non-likely fathers). Paternity concentration may be used by female hamadryas baboons [55], who may ensure protection against infanticide through (albeit not entirely voluntary) exclusive association with a single protective male. MLS-living colobines, by contrast, appear to employ paternity confusion: female golden snub-nosed monkeys copulate with males outside their OMU (but within their band), possibly to reduce the risk of infanticide should one of those males subsequently become the leader of their OMU [56].

The cognitive consequences of MLSs have received attention in few taxa despite the possibility of considerable cognitive capital in these systems due to the presumed necessity of managing relationships across a complex social landscape (*sensu* [57]). It remains premature, however, to view MLS as more cognitively taxing than other social systems, particularly compared to uni-level societies with atomistic fission-fusion [26]. In taxa in which higher levels have a clear social function and require cultivation via affiliative means (e.g. multi-level alliance networks of bottlenose dolphins), selection for social intelligence is expected [58]. On the other hand, the concentration of social interactions within small core units rather than the wider social sphere may have reduced selection for across-the-board social cognition and correspondingly reduced the cognitive load of individuals [59-61]. Evidence of this derives from the presence of MLSs in vulturine guineafowls (*Acryllium vulturinum*), a relatively small-brained bird [62]. The omnipresence of morphological indicators of individual viability in primate MLSs [52], as noted above, as well as behavioural indicators of social levels in cetacean MLSs [63], further suggest a limited need for cognitively-demanding abilities. Using group-level relationships to manage interactions (e.g. treating all members of the same level as mutually substitutable to some extent) and relying

on shared markers to identify social units may release the cognitive challenges of managing tens or hundreds of individual relationships.

MLSs are structurally complex social systems, but the degree to which their individual members also experience **social complexity** remains another open question. The extent to which individuals face social complexity should have a bearing on individual recognition abilities. One recognition route is through vocal communication; thus complex societies may foster vocal complexity [64] in terms of acoustic repertoire size, degree of individuality within discrete calls, and use of signals to identify social units. The evidence in MLSs, however, is mixed. On the one hand, neither geladas nor Guinea baboons show differentiated responses to vocalizations of individuals outside their core units, suggesting that they are either unmotivated or unable to monitor individuals outside their immediate social sphere [65, 66]. Geladas have larger vocal repertoires than baboons [67], but the vocal repertoire of Guinea baboons does not appear more complex than that of non-MLS baboon taxa [68]. On the other hand, African elephants have the neural machinery to vocally distinguish among up to 100 conspecifics [69], and excel at tracking the location of other group members in relation to themselves [70]. Similarly, male bottlenose dolphins in multilevel alliances recognise dozens of individuals from their signature whistles, which are retained for life [71]. These abilities, however, may mask complexity in other modalities (e.g. visual).

Concluding remarks and Future perspectives

Here we have synthesised recent advances in the study of multilevel sociality, proposed a standardised terminology for studies across taxa, and underscored the importance of this topic as a fertile ground for further research (Outstanding Questions). Here, we highlight three promising avenues for future study.

First, the partitioning of the physical landscape among higher levels of MLSs remains poorly understood. In particular, whether and how members of different social levels coordinate their movements, how dispersal opportunities emerge, and how shared spatial preferences (e.g. for sleeping sites) differ from social preferences in producing higher social levels warrant further study. Technologies to collect high-resolution movement, inter-individual

proximity, and social association data [62, 72, 73] can help detect interactions among social units and tease apart the relative effects of the physical and social environments [74]. Additionally, developing empirically grounded and spatially-explicit agent-based models can shed light on the interplay between collective decision-making, movement and social interactions that may underlie the upper and apex social levels.

Second, in addition to group coordination [75], the long-standing question of whether the typical structural complexity of MLS necessitates or promotes higher cognitive abilities deserves further attention. This would also contribute to elucidating the causal links between cognition, social complexity, and communicative complexity [64]. Just because a MLS looks complex from the outside does not mean that it is perceived as such from the inside unless so demonstrated [76]. Comparing the allocation of social attention and inferential reasoning capacities in closely related species that differ in social organisation would be particularly revealing. So far most of the species living in MLSs are large-brained mammals; should MLSs turn out to be more widespread in other groups (e.g. [62]), then this could be evidence that elaborate encephalisation is not a prerequisite for the evolution of MLS.

Third, we currently lack an understanding of how social transmission differs between MLSs and uni-level societies. Theoretical and empirical work has shown that the way social interactions are structured within a single social level can foster or constrain the spread of socially transmitted information and pathogens [77, 78]. Whether core groups in MLSs act as transmission bottlenecks has been virtually unexplored, but could be quantified through experiments whereby problem-solving techniques are seeded in core units and the diffusion (or lack thereof) across unit boundaries is monitored. Similarly, while MLSs can structure the gastrointestinal microbiota [79] that play a role in health and immunity, little is known about how microbiota are transmitted across social levels. Individual microbiome signatures may be obscured by living in a large MLS (as a result of co-habitation of reproductive units and synchronised between-unit behaviour); alternatively, MLSs may crystallise distinct microbiome signatures between units [80]. The dynamics of other physiological states, such as physiological stress, within MLSs also remains an untapped area of research. While stress influences individual behaviour and performance, it is unknown whether belonging to a MLS

buffers animals from stressors or further exposes them to indirect stressors emanating from this wider social environment.

Current evidence for MLSs in larger-bodied animals varies across species, partially due to the lack of consistency in definitions of social levels, both conceptually and analytically. We suggest limiting the use of this terminology to species with a demonstrably bounded core unit structure and frequent or permanent association among core units into one or more recognizable upper levels. These criteria exclude species in which core units either change in composition or encounter one another only occasionally. To facilitate future cross-species comparisons, we also advocate adherence to the terminology herein proposed for the various levels in a MLS.

While superficially similar across taxa, the underlying social dynamics of MLSs—including the role of kinship—can differ fundamentally, reflecting differing evolutionary origins. Coupling socioecology with phylogenetics using a comparative approach (especially between closely related taxa, e.g. Asian vs African elephants) can help elucidate the ecological correlates of the different routes and the role of phylogenetic inertia in MLS maintenance across lineages. The persistence of MLSs is contingent on their benefits (e.g. protection from predators and conspecifics, optimization of gene flow) offsetting their ecological costs. In contrast to a one-size-fits-all group, individuals living in MLS are simultaneously members of multiple levels and can thus experience cost-benefit trade-offs of group living at multiple levels. Finally, living in a MLS brings about novel challenges and exigencies that can influence the evolution of pre-copulatory sexual selection and possibly cognition.

Humans share the same principles of multilevel sociality with other animals (Box 3), thus the study of the evolutionary drivers of MLSs can help elucidate our own evolutionary history. As technology improves the simultaneous tracking and collection of high-definition social and communication data on entire animal groups, it may reveal hitherto hidden social layers in other animal societies. Mapping the taxonomic distribution of multilevel sociality will expand our understanding of its drivers and consequences, providing a valuable reference point for the evolutionary pathways of sociality in our own species.

Box 1: How to identify levels in animal societies

Detecting social levels requires combining qualitative and quantitative methods with high-quality empirical data from long-term studies. Researchers often apply clustering methods

400 to direct observations of social data: interaction rates [14] or frequency of associations of
401 individuals in proximity [10, 13, 72] or temporally clumped [12, 81]. Popular methods
402 include—but are not limited to—network modularity, data cloud geometry, and knot
403 analysis.

404 Modularity measures how well a network of individuals connected by social relationships is
405 structured into densely connected subgroups, with values ~0.3-0.5 representing feasible
406 subdivisions [82, 83]. The Louvain method creates hierarchical subgrouping of individuals
407 iteratively (Fig. IA), maximising the density of connections within versus between groups at
408 each hierarchal level [5, 84]. Data cloud geometry identifies subgroupings at multiple scales
409 with random walks through a network [3]. Hierarchical cluster analysis can be combined
410 with knot analysis displaying the cumulative bifurcations, where significant changes in the
411 rate of bifurcation ('knots') suggest distinct levels [10, 32] (Fig IB). At the population level,
412 these methods can reveal separate social groups [80]; to delineate stable core units, they
413 should be applied at the most inclusive social level.

414 Identifying stable substructuring from preferential associations does not necessarily make a
415 society multilevel. This is contra permissive definitions that "any society in which an
416 individual differentially associates with more than one set of companions is in essence a
417 multilevel society" [85]. We highlight the need for stringent delineations of social levels, in
418 which within-unit social connectivity is significantly higher than between units.

419 It is also necessary to demonstrate that social levels are not artefacts. First, one can use
420 resampling techniques or null models to show how the level delineation differs from
421 random [83]. Subsequently, their biological meaningfulness must be backed up by empirical
422 observations and correspond to groupings derived from naturalistic observations. 'Ground-
423 truthing' is critical, but one should not over-rely on subjective visual impressions, as social
424 units distinguished by observers may not be salient to the animals [76].

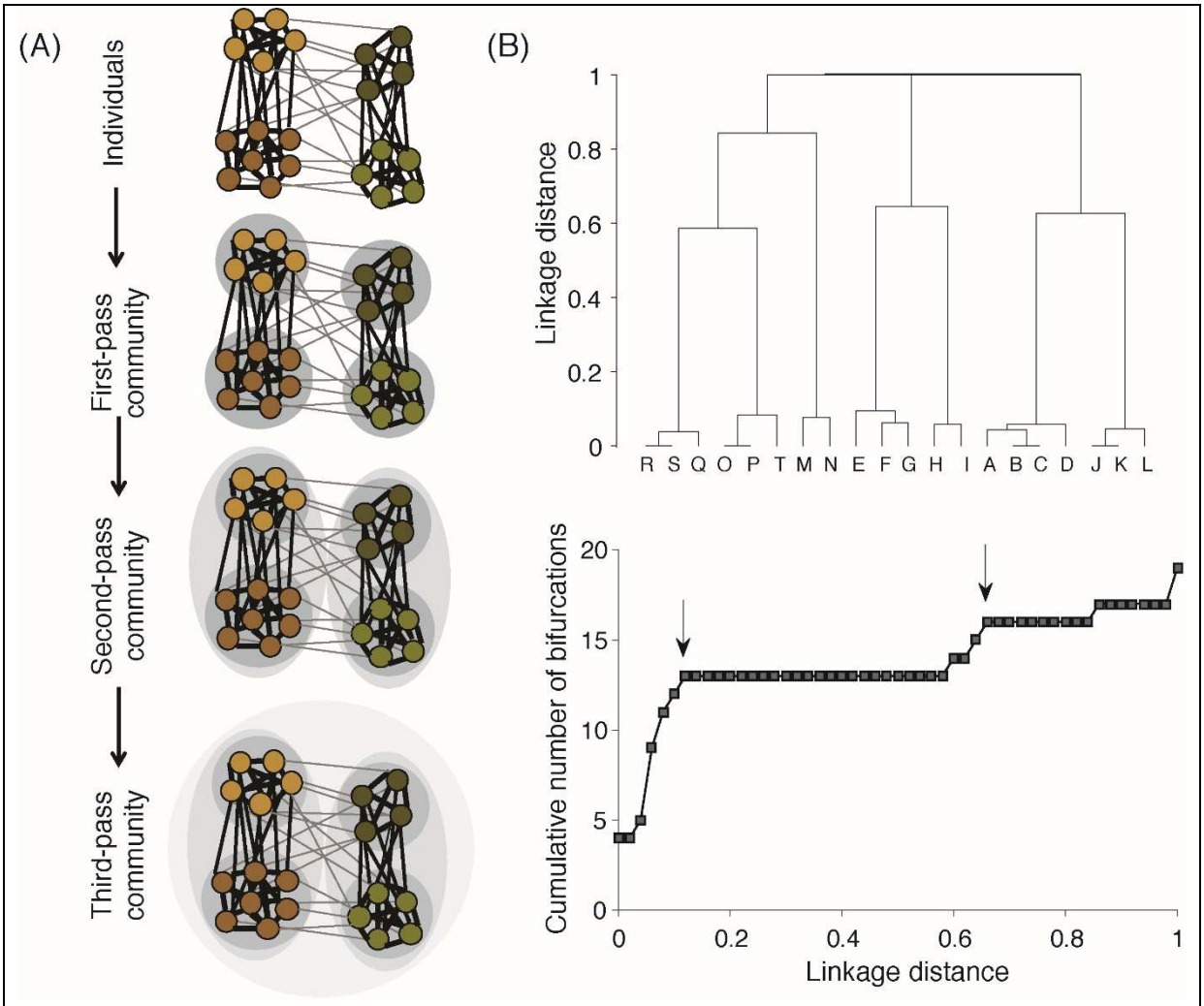

Fig. I: Delineating social levels. A) Louvain method. Individuals strongly connected amongst themselves compose “first-pass communities” (core units); some are strongly connected to one another and detected as “second-pass communities”, until the apex community. B) Hierarchical clustering and knot analysis. Dendrogram in which linkage (here, 1-association index) is depicted by a knot diagram showing the cumulative number of bifurcations (arrows).

Box 2: Culture as a driver of social levels

Rich social lives, experienced within complex societies, can stimulate learning. Animals deal with risks and resources by fine-tuning behaviour; social animals do so by tracing their physical and social environments. Learning new information from conspecifics—and using it collectively—increases within-group cohesion and coordination. Socially-learned behaviours shared within subsets of a population (culture) can in turn modulate social interactions and demarcate social boundaries [77].

How can culture structure well-mixed populations into sympatric yet distinct groups [77]? One route is the feedback between the tendency of similar individuals to associate and the subsequent opportunities to learn from them that promotes within-group behavioural homogeneity. This is leveraged when individuals are conformists or mark their group identity so social interactions occur preferentially among members. With increased behavioural similarity comes social cohesion—groups become tighter as members reinforce their social connections and shred ties with outsiders. This way, culture can—directly or indirectly—erect social barriers and delineate a distinct level in a society. Socio-cultural boundaries are prominent in human societies, but they can also structure non-human societies.

Several animal populations feature sympatric groups with distinct repertoires of socially-learned behaviours, especially foraging tactics and communication signals [86]. Communication is critical in social contexts, thus influential in demarcating social groups. For social animals, learning communication signals correctly is essential to maintain group cohesion, reinforce bonds, and aid collective decision-making. Distinctive signals can be necessary to distinguish social levels, from addressing affiliates to identifying which groups one belongs to [63]. MLSs of toothed whales illustrate how learning communication signals can generate such culturally-driven social levels.

The MLSs of killer and sperm whales contain stable core units and fluid intermediate levels [2] but differ from terrestrial MLS by featuring upper levels (clans) delineated by socially-learned acoustic communication signals. The ‘pulsed call’ dialects of killer whale clans emerge from innovations and learning errors combined with a tendency to diverge from kin

[87]**.** The ‘coda’ dialects of sperm whale clans emerge from biased learning in which conformists learn the most common signals from similar individuals [88]. In both, boundaries around clans are unlikely products of stochastic processes alone—genetic or cultural drift—but instead result from social transmission of behaviour [87, 88], making culture a key ingredient of their MLSs. Finding analogous cultural processes shaping societies of species in completely different environments can help uncoverparallels between human and non-human MLS [86].

Box 3: Multilevel societies in humans

Human MLSs differ from those of other animals in that sets of multiple core units bonded through bilateral kin ties form cooperative networks with high levels of between-group coordination [8, 24, 89]. In hunter-gatherer societies, core family units—mostly monogamous, sometimes polygynous, rarely polygynandrous—are part of relatively fluid local bands of ~50 individuals and of higher-level interconnected multi-camps [90]. The high costs of reproduction in humans has promoted cooperation in food procurement, favouring within-unit food sharing and provisioning, thereby constraining polygyny and male dominance. These patterns, reflected in modern hunter-gatherers [89], are associated with a change in residence patterns from sex-biased dispersal to bi-sexual exogamy: most hunter-gatherer groups are bilocal or multilocal, i.e. both males and females keep close cooperative kin links across camps, helping to offset reproductive costs. Bilateral kin ties bridge between-camp affinities, with nuclear families moving between camps [90, 91]. This social configuration promotes within- and between-camp cooperation and large home ranges, while at the same time producing a new social system where neither sex is closely related to their camp of residence [92]. Clustering at the band level of more closely related households facilitates food sharing and cooperative subsistence [93].

Phylogenetic models suggest that modern human societies originated as multimale-multifemale groups and then evolved into MLSs with one-male core units prior to or during the evolution of pair bonds [48, 89]. The evolution of stable pair bonds may have paved the way for bilateral kin and in-law recognition [94]: once pair bonding was established, shared reproductive interests between affinal (in-law) families would extend cooperation beyond kin, promoting affinal kin recognition [95], and strong between-group ties would be cemented via both consanguineal kinship and affinal kinship (Fig. II). This fluid sociality with frequent mobility between unrelated bands would promote cooperation between unrelated families, through resource sharing [91] and reciprocal allomaternal care [96]. Strong bonds between unrelated families [97] in this vastly extended social landscape would lead to a tenfold greater likelihood of encountering role models for social learning compared to chimpanzees [98]. Frequent opportunities for information exchange and accumulation of

cultural and technological knowledge [99] thus underlie the remarkable success of human MLSs.

A phylogenetic model suggests that human MLSs evolved through a series of transitions from ancestral multimale-multifemale groups to multi-family groups to strongly bonded communities [89].

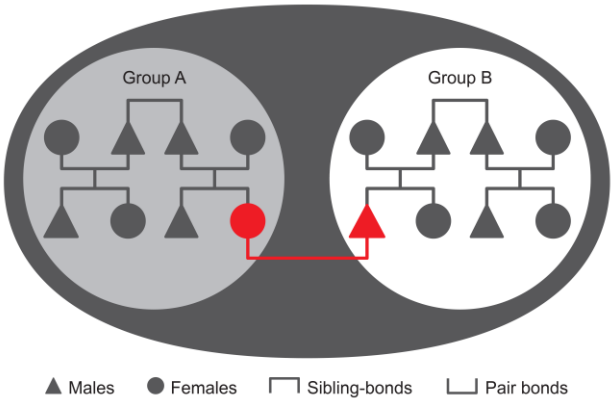

Fig. II. Bilocality with exogamy of males and females and the evolution of human MLSs. The key unit of between-group alliances is a pair bond (red) linking the spouses' kin living in different groups (A, B) and connecting the two sets of in-laws (modified from [100]).

Table 1. Names and approximate sizes of the various levels in the MLS of a representative sample of mammals.

Taxon	*Core unit*		*Intermediate level*		*Upper level*		*Apex level*	
	Designation	**Size**	**Designation**	**Size**	**Designation**	**Size**	**Designation**	**Size**
Gelada (*Theropithecus gelada*)	Unit	2-30	Team	10-50	Band	50-400	Community	50-1500
Hamadryas baboon (*Papio hamadryas*)	OMU	2-10	Clan	10-75	Band	30-400	Troop	100-800
Guinea baboon (*Papio papio*)	Unit	2-10	Party	10-51	Gang	>80	Community	375
Rwenzori colobus (*Colobus angolensis ruwenzorii*)	Core unit	4-23	Clan	37-88	Band	135-512		
Snub-nosed monkeys (*Rhinopithecus* spp.)	OMU	9			Band	22-480	(Troop)	
Hunter-gatherer humans (*Homo sapiens*)	Family	5	Extended family	15	Band	50	Community, mega-band, tribe	150-1500
Plains zebra (*Equus quagga*)	'Harem'	5			Herd	42		
African elephant (*Loxodonta africana*)	Family	8			Bond group	16	Clan	34
Sperm whale (*Physeter macrocephalus*)	Social unit	6-12	Group	7-32	Clan	>1000		

OMU = one-male unit. Ranges are given where there is dramatic variation in level sizes.

555 **Fig. 1. Multilevel society as a nested assemblage of at least two discernible social levels**
556 **between individual and population**. Individuals represented by nodes are connected by
557 links representing social interactions and/or relationships. The *core units* and *upper level* are
558 the two mandatory social levels, while (one or more) *intermediate levels* and the *apex level*
559 are facultative levels. *Core units* are more cohesive than the higher social levels, which vary
560 in stability and cohesiveness.

561

562

563

564 **Fig. 2. Distribution of multilevel societies (MLS) across the mammalian phylogenetic tree.**
565 Phylogram based on [101] shows taxa with strong and likely evidence of MLSs, illustrated by
566 African savanna elephants (*Loxodonta africana* [10]; photo: C. Schradin); Guinea baboons
567 (*Papio papio* [43]; photo: J. Fischer); hamadryas baboons (*Papio hamadryas* [17]; photo: L.
568 Swedell); geladas (*Theropithecus gelada* [13]; photo: T. Bergman); proboscis monkeys
569 (*Nasalis larvatus* [102]; photo: I. Matsuda); black-and-white snub-nosed monkeys
570 (*Rhinopithecus bieti* [12]; photo: C. C. Grueter); Rwenzori black-and-white colobus (*Colobus*
571 *angolensis ruwenzorii* [6, 103]; photo: C. C. Grueter); plains zebras (*Equus quagga* [29];
572 photo: D. Rubenstein); and sperm whales (*Physeter macrocephalus* [2]; photo: A. Cotton).
573 Additional taxa with MLS include long-finned pilot whales (*Globicephala melas*) [104], short-
574 finned pilot whales (*Globicephala macrorhynchus*) [4], orca or killer whales (*Orcinus orca*)
575 ([105]; but see [106]), Asian elephants (*Elephas maximus*) [5], Gobi khulans (*Equus*
576 *hemionus*) [107], all other species of snub-nosed monkeys (*Rhinopithecus* spp.) [30], douc
577 langurs (*Pygathrix* spp.) [108], and humans [31]. MLSs may also occur in uakaris (*Cacajao*
578 spp.) [109] and drills (*Mandrillus leucophaeus*) [110] but our knowledge of the social
579 organisation of these taxa in the wild is limited.
580

581

582

583

584 ***Glossary***

585 Aggregation: Temporary gathering of individuals and units that is usually the result of some
586 nonsocial forcing factor, e.g. localised resources.

587 Fission-fusion (dynamics): Spatiotemporal variation in cohesion of group members and
588 subgroup size and composition.

589 Multilevel society: A social system composed of nested social entities comprising a
590 minimum of two discernible levels of social integration between the individual and the
591 population—*core units* and *upper level*. The primary entities are small core units that are
592 usually stable over time; through proximity maintenance and activity coordination with
593 other core units they form (at least one more) successively higher levels of grouping.

594 Multilevel alliance: Alliances are temporally stable coalitions of two or more individuals
595 acting cooperatively against a third party; in a multilevel alliance system, context-dependent
596 competitive interactions between alliances are found on several hierarchical, more inclusive
597 levels.

598 Social complexity: The number of differentiated relationships as well as the extent of
599 relationship differentiation that exists within a society.

600 Social organisation: Size and demographic composition of a social group.

601 Social structure: Content, quality, and patterning of social relationships emerging from
602 repeated interactions between pairs of individuals belonging to a social group.

603 Social system: The social organisation, social structure, care and mating system of and
604 among the social units of a given population or species.

605 Core unit: A set of individuals in (nearly) permanent mutual association; in MLSs 'core unit'
606 is used for the first grouping level; core units in MLSs are to a certain degree behaviourally
607 self-contained over all relevant time scales, so that the majority of interactions and
608 associations occur within, rather than between, units.

609

610

Acknowledgments

CCG would like to acknowledge the late Hans Kummer (1930-2013) for igniting his passion for multilevel societies and Carel van Schaik for a decade and a half of inspiration and guidance. LS would also like to thank Hans Kummer for his inspirational work on hamadryas baboons that laid the groundwork for decades of research on this fascinating taxon. We thank Richard Connor, Damien Farine, Hal Whitehead, Giovanni Forcina, and the anonymous reviewers for helpful comments and discussions.

References

1. Clutton-Brock, T.H. (2016) Mammal Societies, John Wiley & Sons.
2. Whitehead, H. et al. (2012) Multilevel societies of female sperm whales (*Physeter macrocephalus*) in the Atlantic and Pacific: why are they so different? Int J Primatol 33, 1142–1164.
3. VanderWaal, K.L. et al. (2014) Multilevel social organization and space use in reticulated giraffe (*Giraffa camelopardalis*). Behav Ecol 25, 17-26.
4. Mahaffy, S.D. et al. (2015) High site fidelity, strong associations, and long-term bonds: Short-finned pilot whales off the island of Hawai'i. Mar Mamm Sci 31, 1427-1451.
5. Nandini, S. et al. (2018) Group size differences may mask underlying similarities in social structure: A comparison of female elephant societies. Behav Ecol 29, 145-159.
6. Stead, S.M. and Teichroeb, J.A. (2019) A multi-level society comprised of one-male and multi-male core units in an African colobine (*Colobus angolensis ruwenzorii*). PLoS ONE 10, e0217666.
7. Morrison, R.E. et al. (2019) Hierarchical social modularity in gorillas. Proc R Soc B 286, 20190681.
8. Grueter, C.C. et al. (2012) Evolution of multilevel societies in nonhuman primates and humans. Int J Primatol 33, 1002-1037.
9. Whitehead, H. (2003) Sperm Whales: Social Evolution in the Ocean, University of Chicago Press

10. Wittemyer, G. et al. (2005) The socioecology of elephants: Analysis of the processes creating multitiered social structures Anim Behav 69 1357-1371
11. Dunbar, R.I.M. and Dunbar, E.P. (1975) Social Dynamics of Gelada Baboons, Karger.
12. Grueter, C.C. et al. (2017) Deciphering the social organization and structure of wild Yunnan snub-nosed monkeys (*Rhinopithecus bieti*). Folia Primatol 88, 358-383.
13. Snyder-Mackler, N. et al. (2012) Defining higher levels in a gelada multilevel society. Int J Primatol 33, 1054-1068.
14. Schreier, A.L. and Swedell, L. (2009) The fourth level of social structure in a multi-level society: ecological and social functions of clans in hamadryas baboons. Am J Primatol 71, 948-955.
15. Schreier, A.L. and Swedell, L. (2012) Ecology and sociality in a multilevel society: ecological determinants of spatial cohesion in hamadryas baboons. Am J Phys Anthropol 148, 580-588.
16. Abegglen, J. (1984) On Socialization in Hamadryas Baboons: A Field Study, Bucknell University Press.
17. Kummer, H. (1968) Social Organization of Hamadryas Baboons: A Field Study, The University of Chicago Press.
18. Zhang, P. et al. (2008) Female social dynamics in a provisioned free-ranging band of the Sichuan snub-nosed monkey (*Rhinopithecus roxellana*) in the Qinling Mounains, China Am J Primatol 70, 1013-1022.
19. Swedell, L. (2002) Affiliation among females in wild Hamadryas baboons (*Papio hamadryas hamadryas*). Int J Primatol 23, 1205-1226.
20. Xiang, Z. et al. (2014) Males collectively defend their one-male units against bachelor males in a multi-level primate society. Am J Primatol 76, 609-617.
21. Gersick, A.S. and Rubenstein, D.I. (2017) Physiology modulates social flexibility and collective behaviour in equids and other large ungulates. Phil Trans R Soc B 372, 1727.
22. Guo, S. et al. (2010) The mating system of the Sichuan snub-nosed monkey (*Rhinopithecus roxellana*). Am J Primatol 72, 25-32.
23. Grueter, C.C. and van Schaik, C.P. (2010) Evolutionary determinants of modular societies in colobines. Behav Ecol 21, 63-71.
24. Grueter, C.C. and White, D.R. (2014) On the emergence of large-scale human social integration and its antecedents in primates. Structure and Dynamics 7, 1-27.

672 25. Pisor, A.C. and Surbeck, M. (2019) The evolution of intergroup tolerance in nonhuman
673 primates and humans. Evol Anhropol 28, 210-223.
674 26. Aureli, F. et al. (2008) Fission-fusion dynamics: New research frameworks. Curr
675 Anthropol 49, 627-654.
676 27. Chapman, C.A. et al. (1995) Ecological constraints on group size: an analysis of spider
677 monkey and chimpanzee subgroups. Behav Ecol Sociobiol 36, 59-70.
678 28. Rodseth, L. et al. (1991) The human community as a primate society. Curr Anthropol 32,
679 221-254.
680 29. Rubenstein, D.I. and Hack, M. (2004) Natural and sexual selection and the evolution of
681 multi-level societies: insights from zebras with comparisons to primates. In Sexual Selection
682 in Primates: New and Comparative Perspectives (Kappeler, P.M. and van Schaik, C.P. eds),
683 pp. 266-279, Cambridge University Press.
684 30. Kirkpatrick, R.C. and Grueter, C.C. (2010) Snub-nosed monkeys: Multilevel societies
685 across varied environments Evol Anthropol 19, 98-113.
686 31. Hamilton, M.J. et al. (2007) The complex structure of hunter–gatherer social networks.
687 Proc R Soc B 274, 2195-2202.
688 32. Beck, S. et al. (2011) The influence of ecology on sociality in the killer whale (*Orcinus*
689 *orca*). Behav Ecol 23, 246-253.
690 33. Wiszniewski, J. et al. (2009) Social cohesion in a hierarchically structured embayment
691 population of Indo-Pacific bottlenose dolphins. Anim Behav 77, 1449–1457.
692 34. Connor, R.C. and Krützen, M. (2015) Male dolphin alliances in Shark Bay: Changing
693 perspectives in a 30-year study. Anim Behav 103, 223-235.
694 35. Forcina, G. et al. (2019) From groups to communities in western lowland gorillas. Proc R
695 Soc B 286, 20182019.
696 36. Snyder-Mackler, N. et al. (2014) The socio-genetics of a complex society: female gelada
697 relatedness patterns mirror association patterns in a multilevel society. Mol Ecol 23, 6179-
698 6191.
699 37. Swedell, L. and Schreier, A. (2009) Male aggression towards females in hamadryas
700 baboons: conditioning, coercion, and control. In Sexual Coercion in Primates and Humans:
701 An Evolutionary Perspective on Male Aggression against Females (Muller, M.N. and W., W.R.
702 eds), pp. 244-268, Harvard University Press.

703 38. Städele, V. et al. (2015) Fine-scale genetic assessment of sex-specific dispersal patterns
704 in a multilevel primate society. J Hum Evol 78, 103-113.
705 39. Fischer, J. et al. (2017) Charting the neglected West: The social system of Guinea
706 baboons. Am J Phys Anthropol 162, 15-31.
707 40. Pappano, D.J. et al. (2012) Social 'predators' within a multilevel primate society. Anim
708 Behav 84, 653-658.
709 41. Qi, X. et al. (2017) Male cooperation for breeding opportunities contributes to the
710 evolution of multilevel societies. Proc R Soc B 284, 20171480.
711 42. Swedell, L. and Plummer, T. (2012) A papionin multi-level society as a model for early
712 hominin evolution. Int J Primatol 33, 1165-1193.
713 43. Patzelt, A. et al. (2014) Male tolerance and male-male bonds in a multilevel primate
714 society. Proc Natl Acad Sci 111, 14740-14745.
715 44. Städele, V. et al. (2016) The ties that bind: Maternal kin bias in a multilevel society
716 despite natal dispersal by both sexes. Am J Primatol 78, 731-744.
717 45. Tong, W. et al. (2015) Genetic relatedness in two-tiered plains zebra societies suggests
718 that females choose to associate with kin. Behaviour 152, 2059–2078.
719 46. Archie, E.A. et al. (2006) The ties that bind: genetic relatedness predicts the fission and
720 fusion of social groups in wild African elephants. Proc R Soc B, 273, 513-522.
721 47. Konrad, C.M. et al. (2018) Kinship influences sperm whale social organization within, but
722 generally not among, social units. R Soc Open Sci 5, 180914.
723 48. Swedell, L. and Plummer, T. (2019) Social evolution in Plio-Pleistocene hominins: Insights
724 from hamadryas baboons and paleoecology. J Hum Evol 137, 102667.
725 49. Roscoe, P.B. (2009) Social signaling and the organization of small-scale society: the case
726 of contact-era New Guinea. J Archaeol Meth Theor 16, 69-116.
727 50. Fischhoff, I.R. et al. (2007) Social relationships and reproductive state influence
728 leadership roles in movements of plains zebra, *Equus burchellii*. Anim Behav 73, 825-831.
729 51. Grueter, C.C. and van Schaik, C.P. (2009) Sexual size dimorphism in Asian colobines
730 revisited. Am J Primatol 71, 609-616.
731 52. Grueter, C.C. et al. (2015) Are badges of status adaptive in large complex primate
732 groups? Evol Hum Behav 36, 398-406.
733 53. Sheehan, M.J. and Bergman, T.J. (2016) Is there an evolutionary trade-off between
734 quality signaling and social recognition? Behav Ecol 27, 2-13.

735 54. van Schaik, C.P. et al. (1999) Sex and social evolution in primates. In Comparative
736 Primate Socioecology, pp. 204-231, Cambridge University Press.
737 55. Swedell, L. and Saunders, J. (2006) Infant mortality, paternity certainty, and female
738 reproductive strategies in hamadryas baboons. In Reproduction and Fitness in Baboons:
739 Behavioral, Ecological, and Life History Perspectives, pp. 19-51, Springer.
740 56. Qi, X. et al. (2020) Multilevel societies facilitate infanticide avoidance through increased
741 extrapair matings. Anim Behav 161, 127-137.
742 57. Dunbar, R.I.M. (1998) The social brain hypothesis. Evol Anthropol 6, 178-190.
743 58. Connor, R.C. (2007) Dolphin social intelligence: complex alliance relationships in
744 bottlenose dolphins and a consideration of selective environments for extreme brain size
745 evolution in mammals. Phil Trans R Soc B 362, 587-602.
746 59. Tan, J. et al. (2014) Testing the cognition of the forgotten colobines: a first look at golden
747 snub-nosed monkeys (*Rhinopithecus roxellana*). Int J Primatol 35, 376-393.
748 60. Hobson, E.A. et al. (2019) Rethinking animal social complexity measures with the help of
749 complex systems concepts. Anim Behav 155, 287-296.
750 61. Bergman, T.J. and Beehner, J.C. (2015) Measuring social complexity. Anim Behav 103,
751 203-209.
752 62. Papageorgiou, D. et al. (2019) The multilevel society of a small-brained bird. Curr Biol 29,
753 R1120-R1121.
754 63. Gero, S. et al. (2016) Individual, unit and vocal clan level identity cues in sperm whale
755 codas. R Soc Open Sci 3, 150372.
756 64. Peckre, L. et al. (2019) Clarifying and expanding the social complexity hypothesis for
757 communicative complexity. Behav Ecol Sociobiol 73, 11.
758 65. Maciej, P. et al. (2013) Social monitoring in a multilevel society: A playback study with
759 male Guinea baboons. Behav Ecol Sociobiol 67, 61-68.
760 66. Bergman, T.J. (2010) Experimental evidence for limited vocal recognition in a wild
761 primate: implications for the social complexity hypothesis. Proc R Soc B 277, 3045–3053.
762 67. Gustison, M.L. et al. (2012) Derived vocalizations of geladas (*Theropithecus gelada*) and
763 the evolution of vocal complexity in primates. Phil Trans R Soc B 367, 1847-1859.
764 68. Maciej, P. et al. (2013) Vocal communication in a complex multi-level society:
765 Constrained acoustic structure and flexible call usage in Guinea baboons. Front Zool 10, 58.

69. McComb, K. et al. (2000) Unusually extensive networks of vocal recognition in African elephants. Anim Behav 59, 1103-1109.
70. Bates, L.A. et al. (2008) African elephants have expectations about the locations of out-of-sight family members. Biol Lett 4, 34-36.
71. King, S.L. et al. (2018) Bottlenose dolphins retain individual vocal labels in multi-level alliances. Curr Biol 28, 1993-1999.
72. Qi, X. et al. (2014) Satellite telemetry and social modeling offer new insights into the origin of primate multilevel societies. Nat Comm 5, 5296.
73. Hofman, M.P.G. et al. (2019) Right on track? Performance of satellite telemetry in terrestrial wildlife research. PLoS ONE 14, e0216223.
74. He, P. et al. (2019) The role of habitat configuration in shaping social structure: a gap in studies of animal social complexity. Behav Ecol Sociobiol 73, 9.
75. Montanari, D. et al. (2019) Coordination during group departures and group progressions in the tolerant multilevel society of wild Guinea baboons (*Papio papio*). bioRxiv, 797761.
76. Aureli, F. and Schino, G. (2019) Social complexity from within: How individuals experience the structure and organization of their groups. Behav Ecol Sociobiol 73, 6.
77. Cantor, M. and Whitehead, H. (2013) The interplay between social networks and culture: theoretically and among whales and dolphins. Phil Trans R Soc B 368, 20120340.
78. Nunn, C.L. et al. (2015) Infectious disease and group size: More than just a numbers game. Phil Trans R Soc B 370, 20140111.
79. Trosvik, P. et al. (2018) Multilevel social structure and diet shape the gut microbiota of the gelada monkey, the only grazing primate. Microbiome 6, 84.
80. Perofsky, A.C. et al. (2017) Hierarchical social networks shape gut microbial composition in wild Verreaux's sifaka. Proc R Soc B 284, 20172274.
81. Krause, J. et al. (2013) Reality mining of animal social systems. TREE 28, 541-551.
82. Newman, M. (2006) Modularity and community structure in networks. Proc Natl Acad Sci 103, 8577-8582.
83. Shizuka, D. and Farine, D.R. (2016) Measuring the robustness of network community structure using assortativity Anim Behav 112, 237-246.
84. Blondel, V.D. et al. (2008) Fast unfolding of communities in large networks. J Stat Mech: Theor Exp 10, P10008.

798 85. de Silva, S. and Wittemyer, G. (2012) A comparison of social organization in Asian
799 elephants and African savannah elephants. Int J Primatol 33, 1125-1141.
800 86. Whitehead, H. and Rendell, L. (2014) The Cultural Lives of Whales and Dolphins,
801 University of Chicago Press.
802 87. Filatova, O.A. and Miller, P.J. (2015) An agent-based model of dialect evolution in killer
803 whales. J Theor Biol 373, 82-91.
804 88. Cantor, M. et al. (2015) Multilevel animal societies can emerge from cultural
805 transmission. Nat Comm 6, 8091.
806 89. Chapais, B. (2013) Monogamy, strongly bonded groups, and the evolution of human
807 social structure. Evol Anthropol 22, 52-65.
808 90. Kelly, R.L. (2013) The Lifeways of Hunter-Gatherers: The Foraging Spectrum, Cambridge
809 University Press.
810 91. Lewis, H.M. et al. (2014) High mobility explains demand sharing and enforced
811 cooperation in egalitarian hunter-gatherers. Nat Comm 5, 5789.
812 92. Dyble, M. et al. (2015) Sex equality can explain the unique social structure of hunter-
813 gatherer bands. Science 348, 796-798.
814 93. Dyble, M. et al. (2016) Networks of food sharing reveal the functional significance of
815 multilevel sociality in two hunter-gatherer groups. Curr Biol 26, 2017–2021.
816 94. Chapais, B. (2008) Primeval Kinship: How Pair-bonding Gave Birth to Human Society,
817 Harvard University Press.
818 95. Dyble, M. et al. (2018) Inclusive fitness for in-laws. Biol Lett 14, 20180515.
819 96. Page, A.E. et al. (2019) Testing adaptive hypotheses of alloparenting in Agta foragers.
820 Nat Hum Behav 3, 1154–1163.
821 97. Migliano, A.B. et al. (2017) Characterization of hunter-gatherer networks and
822 implications for cumulative culture. Nat Hum Behav 1, 0043.
823 98. Hill, K.R. et al. (2014) Hunter-gatherer inter-band interaction rates: implications for
824 cumulative culture PLoS ONE 9, e102806.
825 99. Salali, G.D. et al. (2016) Knowledge-sharing networks in hunter-gatherers and the
826 evolution of cumulative culture. Cur Biol 26, 2516-2521.
827 100. Chapais, B. (2011) The deep social structure of humankind. Science 331, 1276-1277.
828 101. Meredith, R.W. et al. (2011) Impacts of the Cretaceous terrestrial tevolution and KPg
829 extinction on mammal diversification. Science 334, 521-524.

102. Yeager, C.P. (1990) Proboscis monkey (*Nasalis larvatus*) social organization: group structure. Am J Primatol 20, 95-106.
103. Miller, A. et al. (2020) Spatiotemporal association patterns in a supergroup of Rwenzori black-and-white colobus (*Colobus angolensis ruwenzorii*) are consistent with a multilevel society. Am J Primatol https://doi.org/10.1002/ajp.23127.
104. de Stephanis, R. et al. (2008) Long-term social structure of long-finned pilot whales (*Globicephala melas*) in the Strait of Gibraltar. Acta Ethol 11, 81-94.
105. Bigg, M.A. et al. (1990) Social organization and genealogy of resident killer whales (*Orcinus orca*) in the coastal waters of British Columbia and Washington State. Report of the International Whaling Commission Special Issue 12, 383–405.
106. Tavares, S.B. et al. (2016) A multilevel society of herring-eating killer whales indicates adaptation to prey characteristics. Behav Ecol 28, 500-514.
107. Feh, C. et al. (2001) Ecology and social structure of the Gobi khulan Equus hemionus subsp in the Gobi B National Park, Mongolia. Biol Cons 101, 51-61.
108. Grueter, C.C. et al. (in press) Ecology and behaviour of odd-nosed colobines. In The Colobines: Natural History, Behaviour and Ecological Diversity (Matsuda, I. et al. eds), Cambridge University Press.
109. Bowler, M. et al. (2012) Multilevel societies in New World primates? Flexibility may characterize the organization of Peruvian red uakaris (*Cacajao calvus ucayalii*). Int J Primatol 33, 1110-1124.
110. Gartlan, J.S. (1970) Preliminary notes on the ecology and behavior of the drill, *Mandrillus leucophaeus* Ritgen, 1824. In Old World Monkeys (Napier, J.R. and Napier, P.H. eds), pp. 445-480, Academic Press.